

## Influence of predator cues on terminal investment in courtship by male *Schizocosa ocreata* (Hentz, 1844) wolf spiders (Araneae: Lycosidae)

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**Abstract.** Sexual signals play a critical role in mate attraction, but fitness benefits of signal production depend on a number of external and internal influences. Sexual signaling can be energetically expensive, and has potential to attract unwanted attention from predators. Male brushlegged wolf spiders, *Schizocosa ocreata* (Hentz, 1844) (Araneae: Lycosidae), actively signal to females in the leaf litter habitat during their spring breeding season, but face a tradeoff between current and future reproduction as the season progresses. The terminal investment hypothesis predicts that with fewer available females, increasing risk of predation, and stronger influence of senescence as the season progresses, males should take greater risks to secure mating. We explored this idea by exposing males of increasing ages to female cues alone or female cues combined with predator cues. We found little or no direct evidence to support the terminal investment hypothesis in this species, in that males across all ages essentially ceased active courtship in the presence of predator cues, that is, there was no age related increase in courtship investment in the presence of predator cues. However, we found distinct evidence of senescence in males based on age-related changes in behavior, which has not previously been directly explored in this species. While males maintained similar levels of active courtship across all age classes (in the absence of predator cues), older males increased their relative investment in maintenance behaviors (grooming) and decreased non-courtship display behaviors such as tapping and leg raises. These findings suggest that studies of male behavior in this species should be carefully designed to control for age-related variation in behavioral response.

**Keywords:** Senescence, predation, age effects, chemical cues, context dependence

Sexual signaling is known to be critical for mate attraction in many species. Individuals produce signals that have been shaped over evolutionary time to maximize transmission, reception, and receiver response (Andersson 1994; Johnstone 1996; Rowe 1999; Bradbury & Vehrencamp 2011). Male sexual signals are often elaborate and conspicuous, potentially indicating male quality to females through size and/or symmetry of traits or degree of courtship vigor (Clutton-Brock & Albon 1979; Parker 1983; Kodrick-Brown & Brown 1984; Hebets & Uetz 1999; Byers et al. 2010). However, sexual signals do not evolve in a vacuum and the fitness benefits associated with signaling are contingent upon both external (ecological/environmental) and internal (physiological) factors. Many studies have shown that male traits favored by females through mate attraction impose energetic costs and/or increased the risk of predation on males (Andersson 1986; Magnhagen 1991; Zuk & Kolluru 1998; Roberts et al. 2007; Cady et al. 2011), but far fewer studies have investigated the combined effects of physiological condition, such as age-related performance declines (i.e., senescence), and external influences (e.g., predator cues) on courtship behavior.

Selection should favor males who respond to internal and external influences in a way that maximizes potential fitness benefits associated with signaling (Bradbury & Vehrencamp 2011; Reichard & Anderson 2015). This is especially true for males that face a declining chance of reproduction due to senescence and/or increasing predation. The terminal investment hypothesis suggests that males who face a tradeoff between current and future reproduction, especially where chances of future reproduction are small, should increasingly

invest effort in high risk/high reward behaviors like active, complex signaling and courtship (Clutton-Brock 1984; Part et al. 1992). Such an investment might increase mortality and/or the influence of senescence (Bonduriansky et al. 2008), but would raise the chances of successful reproduction even when obstacles to reproduction are ever increasing (Clutton-Brock 1984; Bonduriansky et al. 2008).

The brushlegged wolf spider, *Schizocosa ocreata* (Hentz, 1844), has been a rewarding model for the study of sexual signaling and mate choice (Uetz & Roberts 2002; Hebets & Papaj 2005), and can be used as a model for investigating issues of behavioral plasticity and context-dependent signaling (Hebets 2011; Clark et al. 2012). *Schizocosa ocreata* is a common ground-dwelling wolf spider abundant in leaf litter of eastern deciduous forests of North America (Dondale & Redner 1990). Females are cryptic and relatively sedentary within the leaf-litter environment, while males traverse the forest floor and actively seek and court hidden females by displaying complex, multimodal signals (Aspey 1976; Cady 1983; Uetz & Roberts 2002; Uetz et al. 2013). Females select males based on size and symmetry of morphological characters (tufts) as well as aspects of courtship vigor (Uetz & Roberts 2002; Hebets & Papaj 2005; Byers et al. 2010). Female receptivity to male courtship increases until females reach approximately three weeks post adult molt, after which receptivity begins a steady decline with advancing age (Uetz & Norton 2007). Males will mate multiple times given the opportunity in this scramble-competition polygyny system (Norton & Uetz 2005; Uetz & Norton 2007), but females typically mate only once after which they become highly

aggressive toward further mating attempts, attacking and often cannibalizing the male (Uetz & Norton 2007).

The silk draglines and associated chemical cues deposited by females as they move through the environment play a critical role in eliciting male courtship. The cues of a female conspecific elicit male courtship responses even in the absence of the female (Stratton & Uetz 1981), and provide valuable information to males including species identity, female age, and mating status (Roberts & Uetz 2004a, b, 2005). Males can also detect and discriminate heterospecific, potentially predatory spider species, and aggressive, mated female conspecifics by their silk and chemical cues, and have shown a decreased courtship response to potentially dangerous congeners, especially predators (i.e., *Tigrosa* spp., see Persons et al. 2002; Roberts & Uetz 2004b; Fowler-Finn & Hebets 2011). The breeding season of *Schizocosa ocreata* occurs for a relatively brief, 5–8 week period in the spring (May/June), and the relative proportion of available, unmated females decreases while the number of potentially cannibalistic, mated females increases (Roberts unpubl.). Males, therefore, have a decreasing chance of mating and increasing chance of being eaten by aggressive females or heterospecific predators as the season progresses.

Here we investigate the terminal investment hypothesis for male *S. ocreata* by exploring the interaction between physiological condition (age/senescence) and suppression of courtship induced by environmental predator cues. If the terminal investment hypothesis is valid in this species, then males should exhibit plasticity in their courtship behavior in response to external and internal conditions. Males decrease investment in conspicuous courtship behavior in the presence of predator cues in general (Roberts & Uetz 2004b; Fowler-Finn & Hebets 2011), but if males suffer reduced reproductive potential as they age, older age classes will be more likely to engage in risky courtship behavior, that is, courtship in the presence of predator cues. We compared the courtship behavior of males from four different age groups exposed to female cues alone or to combined female and predator cue treatments to determine whether males exhibit a plastic courtship response to either ecological or physiological factors.

## METHODS

**Spider collection and maintenance.**—Juvenile *Schizocosa ocreata* were collected from The Dawes Arboretum, Licking County, Ohio, USA (39.97849°N, 82.41614°W) in late April 2010. Female sub-adult and adult *Tigrosa helluo* (Walckenaer, 1837) were collected from Waterman Farm at The Ohio State University, Franklin County, Ohio, USA (40.01220°N, 83.03937°W) in October 2009 and May 2010. Only female *T. helluo* were used in experiments, as females of this species are considerably larger and generally more likely to attack prey than males or juveniles (Walker & Rypstra 2002), and are known to readily accept *Schizocosa* as prey (Roberts, personal observation). *Schizocosa* were housed individually in plastic containers (540 ml, round), with ~20 mm moistened peat moss as a substrate and *ad libitum* water source, and *Tigrosa* were housed similarly in larger containers (950 ml) with more substrate (~50 mm) to allow burrowing. All individuals were maintained at room temperature (22–25°C), stable humidity,

and a 13:11h light:dark cycle to simulate spring lighting conditions. *Tigrosa helluo* were fed a biotypic diet once a week that included one to two adult crickets and one to two mealworms. *Schizocosa ocreata* were fed twice weekly with three to four fruit flies (*Drosophila melanogaster*) or two to three 1-week-old cricket nymphs (*Acheta domesticus*) as appropriate for their size. All *S. ocreata* were checked daily for ecdysis to determine date of maturation for tracking adult age following the ultimate molt.

**Silk collection and substrate preparation.**—Wolf spiders deposit silk and chemical cues as they traverse their environment, and female cues, even in the absence of females themselves, are known to induce males to court (Stratton & Uetz 1981; Roberts & Uetz 2005; Foelix 2011). Further, silk and chemical cues of *Tigrosa* spp. are known to elicit anti-predator behaviors in this and other wolf spider species (Roberts & Uetz 2004b; Bell et al. 2006; Fowler-Finn & Hebets 2011). In order to induce *S. ocreata* male courtship and/or anti-predator responses, we collected silk and associated cues from conspecific females, and from predatory female *T. helluo*. Prior to each trial, we placed an individual female *S. ocreata* on a clean sheet of filter paper (Fisherbrand, 90 mm diameter, round) in an opaque plastic container (90 mm diameter) and using a small brush, gently induced her to make 50 laps around the outside of the filter paper to standardize the amount of cue material deposited. Female conspecifics used for cue deposition were unmated and ranged in age from two to four weeks post-ultimate molt (period of peak receptivity, see Uetz & Norton 2007). Filter papers used in the predator trials were first laden with conspecific female cues as above, after which we placed individual *T. helluo* on each filter paper and induced them to make 50 laps in the same manner as *S. ocreata* females, depositing their cues on top of the *S. ocreata* cues. Preliminary experiments showed no difference in male signaling behavior resulting from order of cue deposition in predator trials. Individual spiders were used only once for silk deposition and no spider was fed within 24 hours of trials, to both standardize hunger and reduce fecal contamination of cues. All trials occurred within 10 minutes of completing the silk deposition stage.

**Experimental design.**—To test the hypothesis that differences in male age are correlated with differences in courtship behavior in the presence of predator cues, we conducted a two-way MANOVA design experiment with male age (one to four weeks of maturity) and predator cues (present/absent) as factors, individuals as replicates, and behaviors (Table 1) as multiple dependent variables. The cohort of males available for this study all matured within a five day period in order to synchronize age effects and the timing of trials as closely as possible. We selected 90 male *S. ocreata* from the lab population as they molted to maturity and randomly assigned each to one of the eight, age-by-predator cue treatment groups (final sample sizes were approximately 11 per treatment group). We used each male only once within 48 hrs of reaching the appropriate age post adult molt such that males “one week old” were six to eight days post maturity when used in experiments, males two weeks old were 13 to 15 days post maturity, etc.

We conducted behavioral assay trials in clear plastic arenas (250 × 100 × 100 mm) where we placed filter paper disks



Table 1.—Ethogram of male *Schizocosa ocreata* behaviors (adapted from Stratton and Uetz 1986; Delaney et al. 2007).

Behavior	Description
Jerky Tap	Active, visual and seismic courtship where the male locomotes with rapid jerky movements while tapping the forelegs, and occasionally the ventral body surface, on the substrate. Seismic signals in the form of percussion and stridulation are also produced.
Tap	Sometimes called double tap, one or both forelegs actively tapped on the substrate.
Leg Raise	Also called “arch” and/or “wave”, one or both forelegs is raised above parallel to the substrate then lowered without striking the substrate.
Chemoexplore	Exploratory behavior where the anteriolateral palp surfaces are rubbed on the substrate while slowly locomoting.
Grooming	The legs or pedipalps are drawn through the chelicerae, or lateral pairs of legs are brushed together rapidly.
Locomotion	Walking, includes wall climbing.
Stationary	Motionless.

containing cues of female conspecifics, and predators as appropriate, silk side up on the bottom of the arena immediately prior to the onset of each trial. We then carefully deposited males into the arena from above and video-recorded their response to cues for 300s. Following each trial, we removed and discarded the cue disks, cleaned the arena using 70% ethanol and a Kimwipe® to remove any residual chemical or silk cues, and allowed the arena to air dry. All recorded trials were later scored for total duration (s) and frequency (number/300s) of male courtship (Jerky Tap), display (Tap and Leg Raise), exploratory (Chemoexplore), antipredator (Stationary) and other, less common behaviors (Table 1), using a freely available behavioral analysis program, JWatcher (vers. 1.0). We transformed the resulting data appropriately (log total duration and square root frequency), removed outliers, and ran correlation matrices on all possible combinations of dependent variables to meet the assumptions of both MANOVA (Tabachnick & Fidell 2001), and subsequent ANOVA (Martin & Bateson 2007), then analyzed using JMP (vers. 9; SAS Institute).

## RESULTS

Frequency and total duration of behaviors were initially analyzed using MANOVA. The overall model in each case was highly significant (Frequency – Wilks’ Lambda  $F_{49,339.49} =$

5.785,  $P < 0.0001$ ; Total Duration – Wilks’ Lambda  $F_{49,339.49} = 4.779$ ,  $P < 0.0001$ ). There was a significant effect of both male age (Wilks’ Lambda  $F_{21,190.07} = 3.645$ ,  $P < 0.0001$ ) and the presence of predator cues ( $F_{7,66} = 30.611$ ,  $P < 0.0001$ ) on the frequency of male behaviors, and the interaction was significant (Wilks’ Lambda  $F_{21,190.07} = 2.300$ ,  $P = 0.0017$ ). Results were similar for the total duration data where there were significant effects of male age (Wilks’ Lambda  $F_{21,190.07} = 4.379$ ,  $P < 0.0001$ ) and predator cues ( $F_{7,66} = 37.398$ ,  $P < 0.0001$ ) on the total duration of male behaviors, also with a significant interaction (Wilks’ Lambda  $F_{21,190.07} = 3.044$ ,  $P < 0.0001$ ). The MANOVA analysis should be interpreted with caution as we found high negative correlation between the behavior “stationary” and other behavioral states. The accepted solution would be to remove the redundant variable (stationary) from analysis (Tabachnick & Fidell 2001), but since this behavior is also an important antipredator response, we felt strongly that it should be included. Further, the highly significant interaction terms make interpretation of the analysis difficult. For these reasons, we also analyzed each behavior independently using two-way ANOVA with Bonferroni adjustment (Tables 2, 3) (Tabachnick & Fidell 2001).

The presence of predator cues had a strong negative effect on frequency and total duration of active courtship behavior (Jerky Tap) of male *S. ocreata*, irrespective of male age (Tables 2, 3; Fig. 1). Frequency and total duration of Tap, a common

Table 2.—ANOVA results for mean frequency of behavioral bouts (number/300s trial) for male *Schizocosa ocreata*. (\* Indicates significance after Bonferroni correction ( $\alpha=0.007$ ))

		Display Behaviors							
		Jerky Tap		Tap		Leg Raise			
Source	df	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>		
Male Age	3,72	0.082	0.970	7.634	<0.001*	10.413	<0.001*		
Predator Cues	1,72	22.148	<0.001*	18.770	<0.001*	66.929	<0.001*		
Age × Cues	3,72	0.875	0.458	4.201	0.009	6.117	<0.001*		
		Other Behaviors							
		Chemoexplore		Grooming		Locomotion		Stationary	
Source	df	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
Male Age	3,72	1.278	0.289	5.324	0.002*	2.669	0.054	4.264	0.008
Predator Cues	1,72	5.080	0.027	0.000	1.000	17.092	<0.001*	8.599	0.005*
Age × Cues	3,72	0.847	0.473	0.383	0.766	2.734	0.050	2.993	0.036

Table 3.—ANOVA results for mean total duration (s) of behaviors for male *Schizocosa ocreata*. (\* Indicates significance after Bonferroni correction ( $\alpha=0.007$ ))

		Display Behaviors							
		Jerky Tap		Tap		Leg Raise			
Source	df	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>		
Male Age	3,72	0.084	0.968	7.324	<0.001*	12.381	<0.001*		
Predator Cues	1,72	22.401	<0.001*	5.045	0.028	83.359	<0.001*		
Age × Cues	3,72	1.031	0.384	2.253	0.089	7.425	<0.001*		
		Other Behaviors							
		Chemoexplore		Grooming		Locomotion		Stationary	
Source	df	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
Male Age	3,72	0.810	0.487	6.544	<0.001*	2.246	0.090	1.684	0.178
Predator Cues	1,72	0.894	0.348	0.000	1.000	8.362	<0.005*	10.513	0.002*
Age × Cues	3,72	1.094	0.357	1.007	0.395	1.711	0.172	1.315	0.276

male display trait correlated with active courtship, also declined significantly with male age, but was only slightly negatively impacted by the presence of predator cues (Tables 2, 3; Fig. 2). Leg Raises were significantly affected by both increasing male age and predator cues such that the behavior was performed almost exclusively in the presence of predator cues, but declined in both frequency and duration with increasing male age (Tables 2, 3; Fig. 3). The number and duration of bouts of Chemoexploratory behavior was largely unaffected by either predator cues or male age (Tables 2, 3), and while there was no detectable influence of predator cues on grooming, males groomed significantly more often and for longer periods as they aged (Tables 2, 3; Fig. 4). Neither locomotion nor time spent stationary was influenced by male age, but males spent more and longer periods stationary and fewer, shorter periods locomoting in the presence of predator cues (Tables 2, 3).

## DISCUSSION

First, and importantly, the frequency and total duration of active, mate-seeking exploratory behavior (Chemoexplore) was consistent across trials, unaffected by advancing male age or the presence of predator cues (Tables 2, 3), so males were clearly able to detect the presence of conspecific female cues even under the influence of predator cues. All subsequent results, then, are unlikely to be a consequence of "masking" of conspecific female cues by predator cues. As suggested in previous studies of this species (Roberts & Uetz 2004b; Fowler-Finn & Hebets 2011), our results support that male *S. ocreata* are able to detect and respond to cues of potential predators by drastically modifying their behavior, even when no predator is physically present and predator cues are presented along with conflicting conspecific female cues. Further, increasing male age has a strong effect on some, but not all, male behaviors performed in response to female

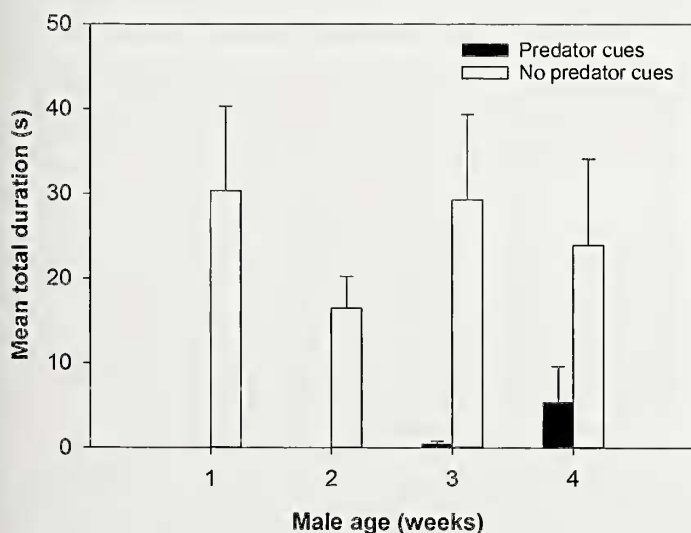


Figure 1.—Mean total duration (s) (+SE) of jerky tap behavior (active courtship) for male *Schizocosa ocreata* exposed to the silk and chemical cues of females in the presence or absence of predator cues.

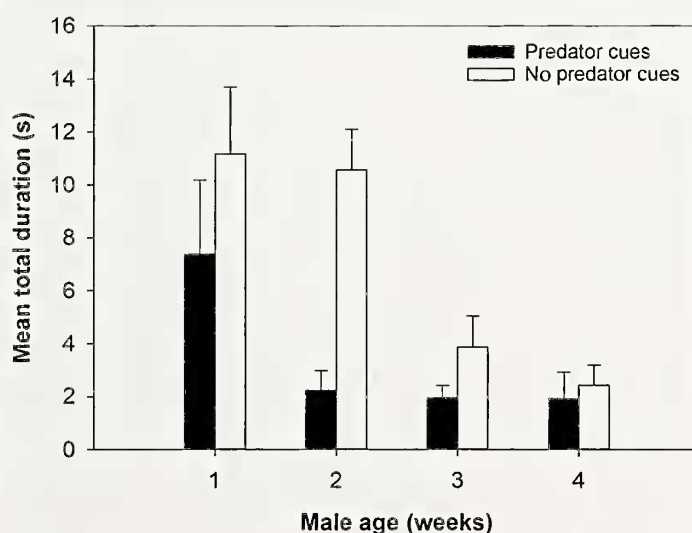


Figure 2.—Mean total duration (s) (+SE) of tapping behavior for male *Schizocosa ocreata* exposed to the silk and chemical cues of females in the presence or absence of predator cues.



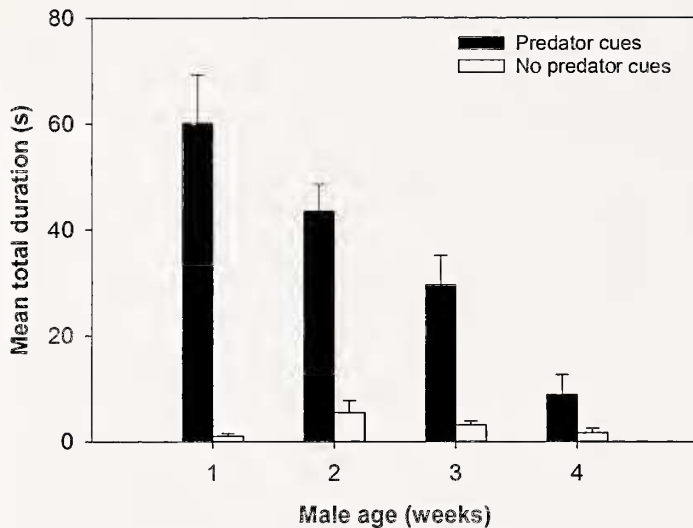


Figure 3.—Mean total duration (s) (+SE) of leg raise behavior for male *Schizocosa ocreata* exposed to the silk and chemical cues of females in the presence or absence of predator cues.

cues. Counter to our terminal investment predictions, we found no meaningful interaction between increasing male age (senescence) and presence of predator cues, suggesting that male *S. ocreata* may not compensate for reduced reproductive potential by increasing use of risky, complex courtship behavior as they age.

Male *S. ocreata* exhibited equivalent levels of active courtship across all age categories when exposed to conspecific female cues alone (Fig. 1), suggesting that male courtship vigor may not measurably senesce with increasing age. Alternatively, and perhaps more likely, males may invest additional resources into active courtship to meet some threshold of vigor generally acceptable to receptive females (Delaney et al. 2007; Shamble et al. 2009; Byers et al. 2010), which is in line with predictions of terminal investment (Clutton-Brock 1984). In stark contrast to the effects of increasing age, males were unlikely to perform the prominent “Jerky Tap” courtship display behavior when cues of predatory *T. helluo* were present (Fig. 1). This does not support terminal investment under influence of predation, but does confirm similar findings of two previous studies. Roberts and Uetz (2004b), as part of an exploration of the species-specificity of female *S. ocreata* chemical cues, found that while males would occasionally court in response to silk and chemical cues of female spiders within, and even far outside, the wolf spider family (Lycosidae), they would not court in response to female *T. helluo* cues. Fowler-Finn and Hebets (2011), using number of body bounces as a proxy for male courtship, found that courtship was greatly reduced in the presence of *Tigrosa* spp. cues. Altogether, the results of these three studies suggest that a significant reduction in active courtship is an anti-predator response in this species. Complex, multimodal courtship by male *S. ocreata*, performed in this context-dependent manner, may benefit males in reproduction but must be severely costly in terms of increased predation risk (Roberts et al. 2007; Roberts & Uetz 2008).

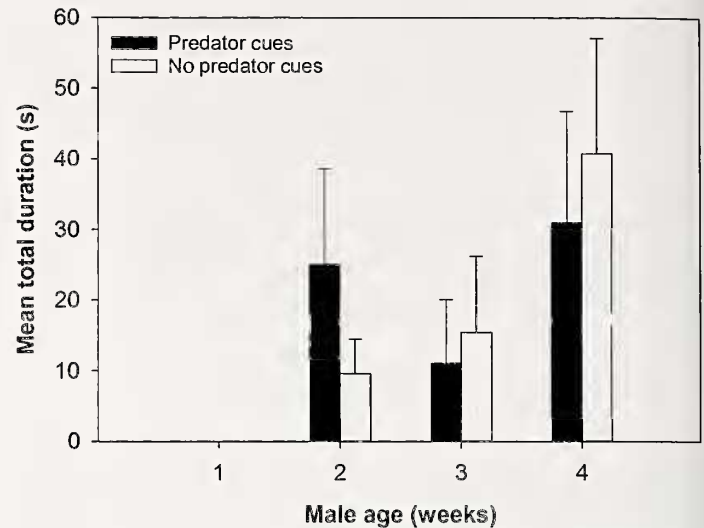


Figure 4.—Mean total duration (s) (+SE) of grooming behavior for male *Schizocosa ocreata* exposed to the silk and chemical cues of females in the presence or absence of predator cues.

While active courtship may be reduced or extinguished in the presence of predator cues across all age groups, younger males (one to two weeks post adult molt) instead adopted other, less “active” display traits (Figs. 2, 3). Leg Raise behaviors were performed almost exclusively in the presence of predator cues (Fig. 3), but were also clear indicators of male senescence with frequency and duration declining significantly with increasing age. Frequency and duration of tapping (Tap) also declined with age, and declined slightly faster in the presence of predator cues (Fig. 2). The most telling indicator of senescence in males is the significant increase in grooming activity with age, whether or not predator cues were present (Fig. 4). Like many spiders, wolf spiders cease molting at maturity (Foelix 2011). Physical traits, such as the tufts of foreleg bristles male *S. ocreata* use in signaling to females, would be subject to wear as males age and thus an increase in maintenance behaviors like grooming is to be expected. Any shift in time allocation to grooming, though, must be balanced by shifts in other behaviors. If males maintain consistent courtship effort as they age, as it appears they do (Fig. 1), then this allocation shift may explain the decline in less critical display behaviors like leg raise or tapping (Figs. 2, 3).

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